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Concept paper

Refining the process of agent selection through understanding plant demography and plant response to herbivory

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Abstract Understanding plant demography and plant response to herbivory is critical to the selection of effective weed biological control agents. We adopt the metaphor of 'filters' to suggest how agent prioritisation may be improved to narrow our choices down to those likely to be most effective in achieving the desired weed management outcome. Models can serve to capture our level of knowledge (or ignorance) about our study system and we illustrate how one type of modelling approach (matrix models) may be useful in identifying the weak link in a plant life cycle by using a hypothetical and an actual weed example (*Parkinsonia aculeata*). Once the vulnerable stage has been identified we propose that studying plant response to herbivory (simulated and/or actual) can help identify the guilds of herbivores to which a plant is most likely to succumb. Taking only potentially effective agents through the filter of host specificity may improve the chances of releasing safe and effective agents. The methods we outline may not always lead us definitively to the successful agent(s), but such an empirical, data-driven approach will make the basis for agent selection explicit and serve as testable hypotheses once agents are released.

Key words agent efficacy, matrix models, *Parkinsonia aculeata*, plant demography, resistance, susceptibility.

INTRODUCTION

Invasive species pose significant threats to biodiversity and primary production (Mack *et al*. 2000; Pimentel *et al*. 2001; Pimentel 2002). Hence regulatory authorities and society in general is becoming risk-averse to introduction of any organisms into a region where they do not naturally occur. This has significant implications for the practice of classical biological control that relies on the introduction of specialist insects and pathogens into novel environments to manage populations of invasive species (Howarth 1991; McFadyen 1998; Sheppard *et al*. 2003; Sheppard & Raghu 2005). There is increasing demand for better evaluation of the risks and benefits of classical biological control agents prior to their introduction (Howarth 1991; Simberloff & Stiling 1996; McEvoy & Coombs 2000; Louda *et al*. 2003a,b; Sheppard 2003; Louda & Stiling 2004; McClay & Balciunas 2006).

Although it is widely acknowledged that classical biological control can be a valuable tool in the management of invasive plants (McFadyen 1998; Thomas & Willis 1998; McEvoy 2002; Hoddle 2004a,b), there is a risk (and an economic cost) attached to introducing a non-native organism. These risks and costs can be reduced if we devise methods that limit the release of ineffective agents. Rather than revisit debates about whether we can be more efficient/rigorous about the way we make agent selection decisions in biological control (e.g. Schroeder & Goeden 1986; Cullen 1992, 1995; Denoth *et al*. 2002; McFadyen 2003; Sheppard 2003), we outline methods that we think could improve the chances of releasing effective agents (Fig. 1). We propose that subjecting the pool of potential agents identified in native range surveys to the filters of plant demography (Briese & Zapater 2002; Briese *et al*. 2002a; Sheppard 2003; Briese 2004; Buckley *et al*. 2005), and responses to herbivory (Broughton 2003; van Kleunen *et al*. 2004; Raghu & Dhileepan 2005) can significantly enhance the likelihood of selecting effective agents. These agents can subsequently be taken through the filter of host-specificity testing (Fig. 1).

PLANT DEMOGRAPHY (FILTER 1)

The structure of plant populations (genetic, spatial, age, size, stage structure) can be used to effectively direct agent selection (Silvertown & Lovett Doust 1993; Crawley 1997). Our objective in weed biological control is to use host-specific insects or pathogens to reduce the growth and/or spread of weed populations to achieve our *a priori* definition of

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'successful management' (van Klinken & Raghu 2006). Ideally we would identify the critical stages that influence the target weed's demography by comparing detailed plant demographic data between the native and invaded range (McEvoy & Coombs 1999; Buckley *et al*. 2005). However, such data are not always available, or logistically possible to collect, in the early stages of a biological control program when agent selection decisions are made. In such circumstances, developing relatively simple models of the target weed's life history based on sound natural history information and any available data on the target (or closely related species) may be extremely valuable.

Matrix models as tools in identifying the Achilles heel of weed populations

Models have been used as tools to understand plant herbivore interactions. In particular matrix models (Caswell 2001) have been used extensively in ecology to identify the most important factors determining a species' population growth or spread. In the context of weed management such models can help identify the vulnerable stage in the weed's life cycle.

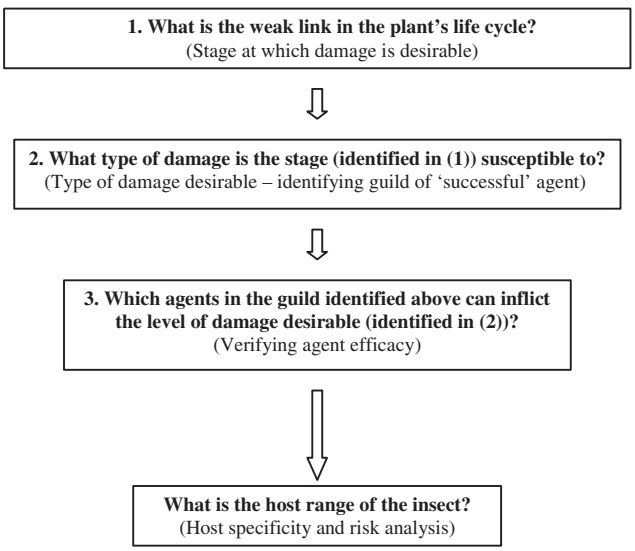


Fig. 1. Nested filters in the agent selection process based on plant (weed) ecology.

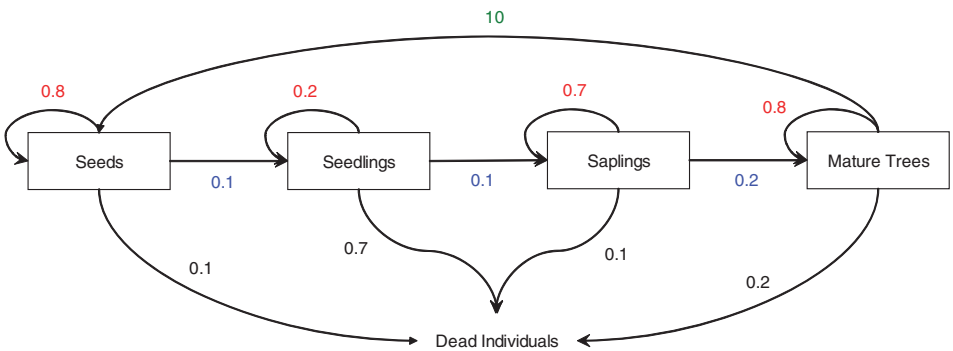
The first step in building a matrix population model is to split the population into a series of non-overlapping classes (e.g. age, size or stage classes) that captures the population structure of the particular weed. Then you need to measure how individuals move between stages (Fig. 2). These parameters can be estimated from tagging and following individuals at a site from year to year (or from month to month for annual species). Alternatively, this may be approximated based on expert opinion and sound natural history observations. The obvious caveat is that the inferences made from the model are only as reliable as the quality of the data and assumptions that went into its construction (e.g. how well the stages represent reasonable 'thresholds', and how the probabilities are fixed with time, space, competitive environment, etc.) (Caswell 2001). A simple example is shown in Figure 2, and the probabilities of moving between stages can be written in matrix form (a transition matrix, Fig. 3).

The population growth rate tends towards a constant and can be determined from the matrix by the dominant eigenvalue. Sensitivity (varying matrix elements by a fixed amount) and elasticity (varying matrix elements by a fixed proportion) analyses indicate the importance of each parameter to the population growth rate (Caswell 2001). Using these analyses we can assess the impact of various control methods (including biological control) on the weed. For example, the thistle *Carduus nutans* was predicted not to be controlled at one site in New Zealand by seed-feeding biological control agents unless additional measures, targeting other life stages, were in place (Shea & Kelly 1998). Equally, such a modelling approach can also be used to assess the impacts on non-target

	Seeds	Seedlings	Saplings	Mature trees
Seeds	0.8	0	0	10
Seedlings	0.1	0.2	0	0
Saplings	0	0.1	0.7	0
Mature trees	0	0	0.2	0.8

Fig. 3. A transition matrix for the hypothetical tree in Figure 2. The elements are colour-coded to match Figure 2 (red indicates survival rates, blue indicates development rates, green indicates reproduction).

Fig. 2. A hypothetical life cycle of a tree. The numbers adjacent to the arrows are the probabilities of an individual moving from one stage to the next. Because individuals survive, grow or die, the probabilities from each stage add up to 1 (except for reproducing individuals where one tree produces many seeds, for example, 10 in this case).



plants by an insect under consideration as a biological control agent (Louda *et al*. 2005).

Constructing a matrix model of Parkinsonia aculeata

As an example of using matrix population models in weed management, we present a model developed for *Parkinsonia aculeata*, a rangeland weed of national significance in Australia.

Identifying discrete life-history stages. The first decision is how to split the population into discrete stages. Obviously seeds fall into a convenient category. However, it is less clear how to separate seedlings and adult plants – by age, by height or by stem/trunk diameter? We chose height as it is a good predictor of seed production and a tree's ability to survive frost and fire. Seedlings and adult plants were split into five categories: 0–1 m; 1–2 m; 2–3 m; 3–5 m; and greater than 5 m.

Calculating demographic parameters. Data collected from Alcoota Station in Central Australia in 2001/2 (van Klinken 2005; L Anderson and S Campbell unpubl. data 2005) were used to derive the different demographic parameters in the transition matrix.

Reproduction – Trees need to be taller than 1 m before they reproduce (Fig. 4a), and there is a clear increase in seed production with height (Fig. 4b). The change in seed production with height is well described by a step function (Fig. 4b). The seed production of each of the height classes was estimated from these relationships (Fig. 5).

Development rate – About 8% of seeds are expected to germinate in any year. The probability of moving between stages (development rates) was estimated from the growth rate curve (Figs 4c,5).

Survival – Smaller trees are less likely to survive frost (Fig. 4d) and so in the transition matrix (Fig. 5), annual mortality declines with plant size. The rate of decay of the seed bank was estimated at about 0.98 per year; this figure includes those seeds germinating at a rate of 0.08 per year (van Klinken 2005; L Anderson and S Campbell unpubl. data 2005).

Based on this transition matrix, the population is expected to grow at this site by 36% every year. The elasticity of this transition matrix can then be calculated (Fig. 6).

The elasticity analysis suggests that the weed is best controlled by removing large trees (>5 m) as they have a massive effect on the population growth rate (Fig. 6). Seed production would have to be reduced by a very high level to create the same effect as cutting down a few large trees. However, the population is sensitive to changes in seed germination rate and the rate of development of young trees.

Logical agent selection decisions can be made based on this information. It is unlikely that an agent is going to inflict mortality on trees greater than 5 m in height on its own. Perhaps an alternate method of control (mechanical/chemical) is required to remove this size class. The elasticity analysis also suggests that seed feeders in this system may not have an

	Seeds	P(0–1)	P(1–2)	P(2–3)	P(3–5)	P(>5)
Seeds	0.02	0	2	86	1206	7586
P(0–1)	0.08	0.02	0	0	0	0
P(1–2)	0	0.08	0.105	0	0	0
P(2–3)	0	0	0.245	0.15	0	0
P(3–5)	0	0	0	0.35	0.56	0
P(>5)	0	0	0	0	0.14	0.95

Fig. 5. Transition matrix for a *Parkinsonia aculeata* population. The elements are colour-coded (red indicates survival rates, blue indicates development rates, green indicates reproduction).

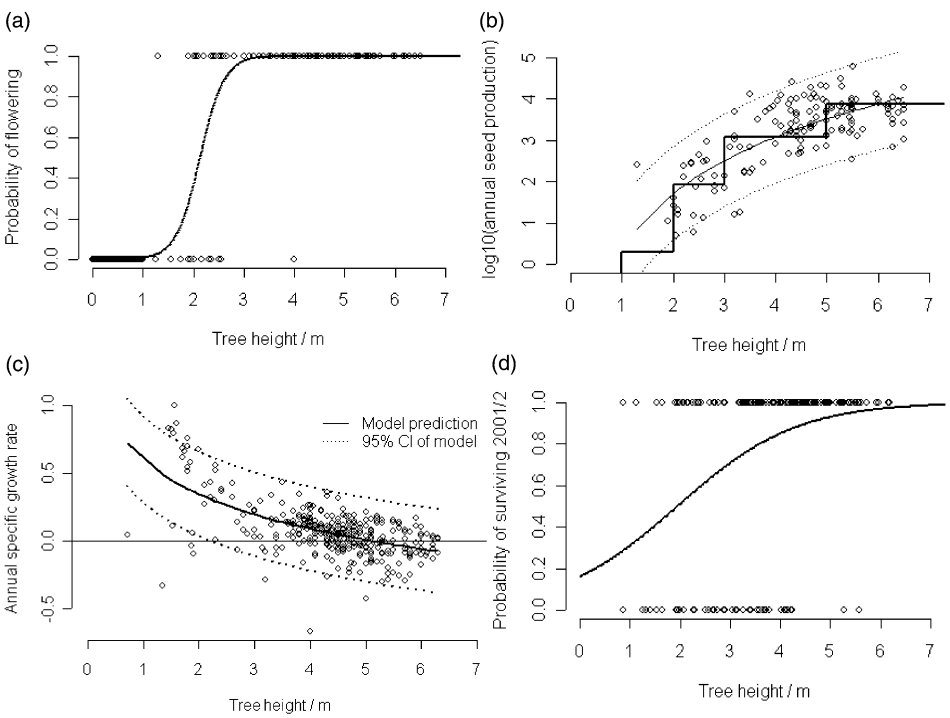


Fig. 4. Effect of tree height on (a) onset of flowering; (b) seed production; (c) growth rate; (d) survival rate. Reproduction is well described by a step function, where the smooth line is the mean and the dotted line is the 95% confidence interval (CI). The other lines are fitted lines, which are used to estimate the parameters of the matrix model for *Parkinsonia aculeata*.

important effect on plant population dynamics. However, the above analysis suggests that affecting the development of young trees can significantly affect population growth rate. This information could serve as the *a priori* basis for selecting biological control agents.

This exercise illustrates how easily a simple model can be used to make predictions in weed management. However, it is important to remember that models are abstractions of the real world. Population dynamics differ year to year and site to site (Shea *et al*. 2005), as is certainly the case for *P. aculeata* in Australia (R van Klinken unpubl. data 2005). Ideally we would like to be able to construct mechanistic models for every system we work on (and there are some excellent programs that assist this process (e.g. DYMEX (Maywald *et al*. 1999)), but in most cases the data requirements are prohibitive. Therefore, matrix models still have a lot to offer as a first step.

The basic matrix models have been adapted in many ways by adding stochastic simulations using a probability distribution for each transition, calculating economic costs so elasticity analysis looks at how spending more money will affect population growth rate, including a matrix of dispersal to look at the spread of invasive species, and including density dependence so that the populations show sensible regulation (Caswell 2001). The main advantage of these models lies in their relative simplicity. They can be rigorously analysed without necessarily requiring large and precise data sets. This sort of approach lends itself quite amenably to the methods required in the process of agent selection.

Once the Achilles heel of the plant's life history has been identified, it is then possible to identify the type of damage that this weak link/transition is most likely to succumb to, by studying plant response to herbivory.

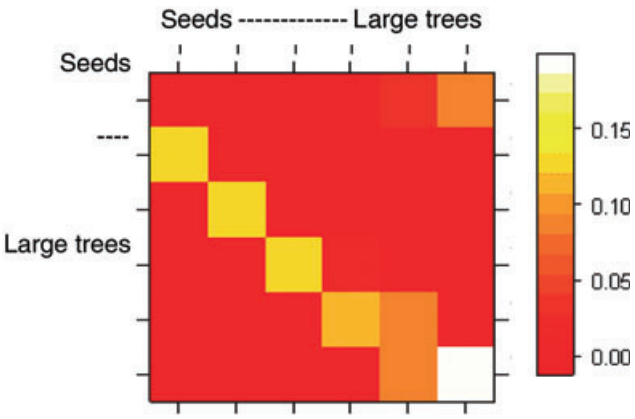


Fig. 6. Elasticity analysis of the transition matrix for *Parkinsonia aculeata* in Central Australia. Each block in the diagram corresponds to a number in the transition matrix. The lighter the colour, the more sensitive the population growth is to a given proportional change in that number.

PLANT RESPONSE TO HERBIVORY (FILTER 2)

Plants experience damage from a wide variety of environmental factors (including herbivores), and exhibit a diversity of responses that can be broadly classified into susceptibility and resistance (Box 1; Belsky *et al*. 1993). From the perspective of selecting a biological control agent, we need to identify the types of damage (that a specialist herbivore can inflict) that results in the management of weed populations.

Ideally, we would like a biological control agent to elicit a plant response of 'susceptibility' (Box 1). Susceptibility is more likely to occur when the plant–herbivore association does not have an evolutionary history, and was the rationale for the 'new associations' model of agent selection (Hokkanen & Pimentel 1989). Susceptibility could also result if the weed has undergone evolutionary change post invasion resulting in a trade-off between growth and/or fecundity, and traits that enable resistance and tolerance (Blossey & Notzold 1995). The frequency of occurrence of such trade-offs is unclear, and it is often difficult to separate from plasticity in response to novel environments (Willis *et al*. 2000; Rogers & Siemann

Box 1 A classification of plant response to herbivory and strategies of plants that confer resistance to minimise damage to tissues (adapted from Belsky *et al*. 1993) and definitions of terms (adapted from Strauss & Agrawal 1999).

Resistance – Plant trait that reduces the preference and/or performance of an herbivore.
- *Avoidance* – A plant trait that reduces the likelihood of interacting with a herbivore or experiencing a negative effect.
  - Escape – A life-history trait that enables a plant to 'avoid' interactions with a herbivore (e.g. dispersal of seeds prior to build-up of seed predator populations (Raghu *et al*. 2005)).
  - Defence – A physical or chemical plant trait that enables the plant to deter herbivore damage and/or negatively influences the fitness of the herbivore (e.g. trichomes or presence of alkaloids).
- *Tolerance* – The degree to which plant fitness is affected by herbivore damage, relative to an undamaged state.
  - Regrowth – The ability of a plant (through either physiological traits or storage organs) to recover from herbivore damage. Regrowth may result in a damaged plant being less fit (undercompensation) as fit (equal compensation) or more fit (overcompensation) in comparison with an undamaged plant.

Susceptibility – The inability of a plant to resist herbivore damage and thereby suffering strongly negative fitness consequences (e.g. reduced growth rate (individual and demographic), low reproductive output).

2002, 2003, 2004; Siemann & Rogers 2003; Bossdorf *et al*. 2004; Maron *et al*. 2004).

Exploration for weed biological control agents typically does not follow the new association model and exploration efforts are often restricted to the target plant's centre of origin (Goolsby *et al*. 2006), where potential agents are likely to have a coevolved interaction with the target plant. Therefore, plant response in these circumstances is likely to encompass the whole gamut of strategies outlined above, with different responses to different types of herbivory (Box 1). In such circumstances it is important to quantify plant response to herbivory to identify the type and extent of damage that an agent needs to inflict to achieve the desired management outcome (Raghu & Dhileepan 2005).

Is it possible to ascertain plant response to different types of herbivory *a priori*?

Once a vulnerable life stage of a weed has been identified, studying response to herbivory can yield valuable information in the context of agent selection. But is it possible to make these decisions without testing the response to every potential insect/pathogen identified on it in the native range? This can be a particularly daunting task in the case of biological control of weeds that have a diverse natural enemy complex. We propose that an alternate approach that simulates herbivory can provide valuable information for agent selection.

Simulated herbivory (mechanical damage to plants that approximates removal of tissues by a herbivore) has a long history of use in ecological research and has been a topic of vibrant debate (Baldwin 1990; Walling 2000; Hjalten 2004; Lehtilä & Boalt 2004). In a recent meta-analysis of 46 published papers on simulated herbivory, Lehtilä and Boalt (2004) found that 68% of the experiments showed differences in some measure of plant response between simulated and actual herbivory while 35% of the statistical analyses in those experiments showed a difference between simulated and actual herbivory. In studies that compared simulated and insect herbivory, 15% of the analyses revealed differences in plant response to the two methods of inflicting damage. When the types of plant response measured was examined, measures of growth and reproduction were less sensitive than other measures to differences in the damage methods with 26% of the analyses showing a difference between the two types of herbivory. Despite these differences, in only 3% of the studies did artificial and natural damage produce opposite plant responses, indicating that the direction of plant response to herbivory can be meaningfully inferred from simulated herbivory trials, while we need to be more cautious about interpreting the magnitude of plant response. In synthesising their findings, Lehtilä and Boalt (2004) concluded, 'the most important effects that artificial damage should succeed in simulating correctly are often the ones affecting biomass and population dynamics of interacting species'.

The advantages of simulated herbivory experiments include the ability to control for type, intensity and frequency of the damage, while simultaneously controlling other confounding effects (Hjalten 2004). The obvious shortcomings include that it is difficult to precisely simulate natural herbivory in terms of the type, distribution and timing of damage and the interactions of damage with other important factors (Hjalten 2004; Lehtilä & Boalt 2004). Furthermore, certain types of physiological associations of herbivores (e.g. galling, other endophagous insects) cannot be simulated. This suggests that the value of simulated herbivory experiments rests with the type of questions being asked. While simulated herbivory may provide valuable clues about plant compensation or tolerance of damage, inferences on more complex ecological interactions are likely to be flawed (Hjalten 2004). Simulated herbivory experiments are less appropriate for understanding the influence of herbivory on higher trophic levels (e.g. parasitoid visitation in response to different plant injury levels), induced plant responses (where insect saliva may be important (Walling 2000)), effects of herbivory on soil processes or changes in competitive effects of plants suffering herbivory with those that are undamaged (Hjalten 2004; Lehtilä & Boalt 2004).

Studying plant response to simulated herbivory to different parts/modules can yield significant ecological insights about compensation and tolerance towards herbivory (Welter 1991; Marquis 1992; Hjalten *et al*. 1993; Welter & Steggall 1993; Foggo 1996; McLaren 1996; Gavloski & Lamb 2000; Tiffin & Inouye 2000; Rogers & Siemann 2002; Sullivan 2003; Hjalten 2004; Lehtilä & Boalt 2004; van Kleunen *et al*. 2004); information that could prove extremely useful in agent selection for weed biological control. Such an approach could help identify the guilds of herbivores most likely to have an impact on plant productivity and growth rates, thereby narrowing the prospective list of biological control agents, and prioritisation of agents in relation to management expectations (Ehler 1998). These studies could also provide guidance to exploration efforts, thereby allowing the limited time available for exploration in the native range to be targeted at the guilds most likely to yield effective agents. These results could also be integrated into models of weed–herbivore interactions to explore likely population level consequences of different types and levels of damage. At the very least, such studies generate hypotheses of the potential efficacy of the different guilds of herbivores (providing an explicit *a priori* basis for selection of particular agents) that can be tested against the performance of biological control agents during quarantine testing and after approval for release (Winder & van Emden 1980; Welter 1991; Broughton 2003; Sullivan 2003; Balciunas 2004; van Kleunen *et al*. 2004; Rebek & O'Neil 2005).

Several recent biological control projects in Australia have benefited from this approach. Simulated herbivory studies on *Mimosa pigra* (giant sensitive tree) in the Northern Territory have been used to generate *a priori* predictions for the performance and likely efficacy of *Macaria pallidata* (Wirf 2006a,b). Similar research on *Alternanthera phylloxeroides* (alligator weed) revealed that the effects of the beetle *Agasicles hygrophilla* could have been reliably predicted (Schooler *et al*. 2006). The response of *Jatropha gossypifolia* (bellyache bush) has provided valuable insights into the way agent

prioritisation decisions need to be made for this species (S Raghu unpubl. data 2005). Detailed experiments on *Macfadyena unguis-cati* (cat's claw creeper) have indicated that a defoliator that is likely to remove at least 75% of the leaf material twice over an 18-week period is the one most likely to control this liana. More significantly though, these simulated herbivory trials suggested that below-ground herbivory is likely to prove counter-productive to the objectives of biological control by triggering vigorous plant compensation. Based on this, leaf feeders are currently being screened for their safety and other guilds of herbivores have been ranked lower (Raghu & Dhileepan 2005; Raghu *et al*. 2006). Studies on *Parthenium hysterophorus* have confirmed that plant response to simulated and actual defoliation is comparable and, therefore, simulated herbivory could have been a tool used in the prioritisation of agents like *Zygogramma bicolorata* (Raghu & Dhileepan 2005). An important point to note is that all the above examples are for leaf-feeding herbivores, highlighting the earlier caveat that the simulated herbivory approach may be more appropriate for ectophagous than endophagous herbivores.

VERIFYING AGENT EFFICACY (FILTER 3)

Once clues about the life stage of the plant to target (Filter 1) and guild a successful herbivore is likely to come from (Filter 2) have been gathered, it is important to assess whether any among the pool of available herbivores can cause the desirable level of damage to achieve the management objective (i.e. our definition of 'successful management') (Fig. 1). There are two components to this. First, it is important to verify whether herbivores in the guild identified can cause the desirable level of damage (for examples of such research on temperate weeds, see Sheppard *et al*. 1994; Briese 1996, 2000, 2006; Swirepik *et al*. 1996; Edwards & Brown 1997; Rees & Paynter 1997; Briese & Zapater 2002; Briese *et al*. 2002a,b, 2003; Zapater *et al*. 2004) and whether plant response to actual herbivory is similar to that identified by simulated herbivory studies (Hjalten 2004; Lehtilä & Boalt 2004). Second, to cause the desired level of damage, the candidate agent may need to attain a certain population density. The former is dealt with in this section, while the latter is dealt with in a subsequent paper (see Zalucki & van Klinken 2006).

At the early stages of a biocontrol program when agent selection decisions are made, any experiments using the candidate agents in the introduced range have to be conducted under quarantine conditions. Detailed tests on host range of agents are undertaken under the confines of quarantine. However, the data collection often stops with identifying host selection decisions made by the insect, and any effects on the plant are usually described qualitatively (e.g. Day *et al*. 1999; Dhileepan *et al*. 2005; Heard *et al*. 2005; Scott & Yeoh 2005). With a little more effort, it is possible to adapt such host-testing studies to gather quantitative data on level of herbivory an agent is able to inflict and the subsequent impacts on the plant in terms of regrowth potential, and in certain circumstances reproductive output (S Raghu *et al*. unpubl. data 2005). Admittedly, the confines of quarantine and small cage testing are likely to overestimate or underestimate the effects of an agent if plants are healthy and growing in optimum conditions. Therefore, exclosure studies or observational data in the weed's native range during exploration efforts could yield additional insights to validate impacts of particular guilds of agents (Sheppard *et al*. 1994; Briese 1996; Swirepik *et al*. 1996; Edwards & Brown 1997; Rees & Paynter 1997; Briese 2000, 2006; Briese & Zapater 2002; Briese *et al*. 2002a,b, 2003; Zapater *et al*. 2004; Hafliger *et al*. 2005). Information on impacts can subsequently be fed-back into matrix models on plant demography to see how these affect population dynamics of the target weed in relation to our management objective. The integration of agent impacts into plant demography models have been used to assess non-target effects (e.g. Louda *et al*. 2005) and for agent evaluation studies (e.g. Shea & Kelly 1998), but can easily be adapted for agent selection.

CONCLUSION – PLACING THE FILTER OF EFFICACY BEFORE THE FILTER OF SAFETY

A central assumption in weed biological control is that specialist herbivores (typically insects, mites and pathogens) can exert a strong top-down influence on plant populations (McFadyen 1998, 2003) in the native range, and the escape from this influence during the process of the plant invading new regions is thought to lead to its invasiveness (referred to as the 'enemy release hypothesis'; Keane & Crawley 2002). This idea is seldom tested prospectively (Maron & Vila 2001) and is often validated retrospectively by the loss of herbivores and pathogens (Mitchell & Power 2003; Torchin *et al*. 2003) and through reference to successful biological control projects (McFadyen 1998, 2003). Through a combination of studies on plant demography and plant response to simulated and/or actual herbivory outlined above, the role of herbivores in regulating plant populations can be explicitly examined *a priori* and any potential role as biological control agents can be evaluated.

We suggest the following sequence of steps, based on plant demography and plant response to herbivory, for refining agent selection decisions in weed biological control.

1 Identify the life-history stage or transitions that when affected have the greatest negative consequence for plant demography.

2 For this vulnerable life stage, understand plant response to herbivory at the level of the individual plant:
   • Use approaches such as simulated herbivory or actual herbivory experiments in the native and introduced ranges to assess plant response (being aware that in the introduced range, the agent is unlikely to have specialist natural enemies).
   • Identify the type and magnitude of damage to which the plant is most vulnerable (i.e. produces the desired effects in relation to the management objective).

3 Prioritise an agent from the guild that causes the type of damage required in (2) to the life stage/transition identified in (1).
   • If (2) was done exclusively using simulated herbivory approaches, treat the findings as testable hypotheses and verify whether plant response to simulated damage and actual herbivore damage is comparable after importing the agent into quarantine, and if possible through native range studies.
4 Proceed to experimentally assessing the specificity of the agent.

We have adopted the metaphor of 'filters' to suggest how agent prioritisation may be improved. Access and taxonomic impediments may be more of a constraint on agent selection decisions in the case of neotropical weeds (see Goolsby *et al*. 2006) than temperate weeds. Therefore, simulating herbivory may be more of a tool in the context of selecting agents for the former. We are also intimately aware that in practice, logistic constraints may force scientists to be unable to subject candidate agents to these filters sequentially. This may not be as critical as ensuring that plant demography and plant response to herbivory be explored in significant empirical detail as a part of deciding which agents to release. As has been demonstrated in the case of research on temperate weeds (Sheppard *et al*. 1994; Briese 1996, 2000, 2006; Swirepik *et al*. 1996; Edwards & Brown 1997; Rees & Paynter 1997; Briese & Zapater 2002; Briese *et al*. 2002a,b, 2003; Zapater *et al*. 2004; Hafliger *et al*. 2005), such an approach offers the possibility of identifying agents that are likely to be effective and safe. At the very least such an approach makes the decisions behind the release of agents explicit, and these can be tested as hypotheses based on the release of agents.

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